

AFRICAN SAVANNAS: BIOLOGICAL SYSTEMS OF HUMIFICATION AND MINERALIZATION

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INTRODUCTION

A number of partial or overall syntheses on African savannas has already been published (e.g. Hopkins, 1965; Bourlière and Hadley, 1970; Anonymous, 1979; Trochain, 1980; Huntley and Walker, 1982; Bourlière, 1983a). They reflect the large amount of researches undertaken in this biome; they also reflect a great heterogeneity in the studied topics, the utilized methods, the sites and periods of study. This amount and heterogeneity, the absence of a clear functional link between all the facies encountered within the entity 'Savanna' preclude any short synthesis, at functional level, embodying the major physical, animal and plant compartments of the savanna.

We therefore have chosen to focus on an aspect, still poorly known though certainly being one of the major mechanisms involved in savanna ecosystems functioning: soil biology in relation to nutrient and matter cycling. This compartment is included in a wider model of savanna functioning centred on primary productivity, presently in elaboration in our laboratory (Clément, 1980; Gonzalez, 1983). This model could be coupled with the one developed by Walker and Noy-Meir (1982) on the grass/tree equilibrium. Walker's model explores the modalities of this equilibrium primarily in relation to water availability but also to nutrient availability and consumption by herbivores. Coupling both models would give a good account of the essential features of African savannas structure and functioning. The conceptual models proposed in this paper refer to the nutrient compartment of the overall model presented in Figure 1. Before focusing on soil functioning, we shall first describe the main characteristics of the African savannas with emphasis on soil.

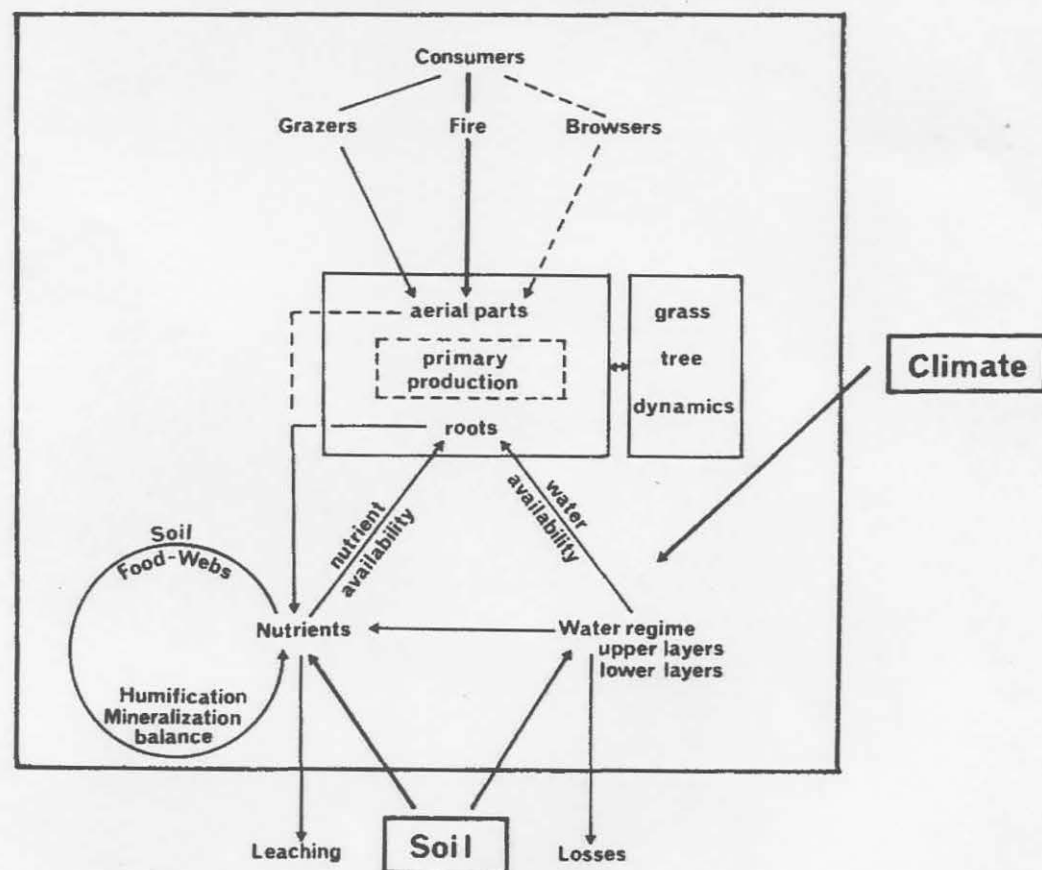


Figure 1. An overall model of savanna functioning.

MAIN FEATURES

African savannas are 'simply defined as those ecosystems which lie between the ... rainforests and the deserts. ... These savannas form a continuum of physiognomic types ranging from closed woodlands ... to treeless edaphic grasslands' (Huntley and Walker, 1982). These types are defined and described, in structure and main ecological traits, in Menaut (1983).

It is a unique feature of Africa to be made of a continuous crystalline shield exposed over large areas and partly covered since the Precambrian by often unaltered sedimentary rocks. When Africa became isolated from the rest of Gondwanaland, a line stretching from central Angola to eastern Sudan divided the continent in north-western flat lowlands, mostly flooded, and in south-eastern faulted dry highlands (Furon, 1968; Grove, 1978). This partition is a fundamental feature of African savannas: its ecological implications are well reflected in climatic differences, in the distribution of vegetation types and certainly in ecosystem functioning.

African savannas extend upon very diverse geological substrates resulting in a great lithological complexity (e.g. FAO-UNESCO, 1977). Three main parent materials may be found.

- The granitized basement complex and metamorphic rocks (gneiss, granite, ...) are distributed all over tropical Africa.
- The consolidated sediments, Clastic sediments (sandstone, siltstone, shale) are mainly found in West Africa and carbonate deposits (limestone, dolomite, marl) make up most of the horn of Africa and some Zambezian highlands.
- The unconsolidated aeolian and alluvial sediments cover the Sahelian region and the core of central and southern Africa. The geologic history of Africa explains its relief dominated by tabular land forms. These results from a long erosion testified by the accumulations of continental deposits. Several erosion cycles have been totally achieved and peneplanation has almost reduced the whole continent to vast and flat surfaces where drainage is disorganized.

It seems reasonable to assume that herbaceous, low, open formations might have spread over Africa even before the break from America (Cretaceous). Pollen records testify since the Upper Tertiary the extension all over tropical Africa of savannas rather similar to the present ones (Van der Hammen, 1983). At the present

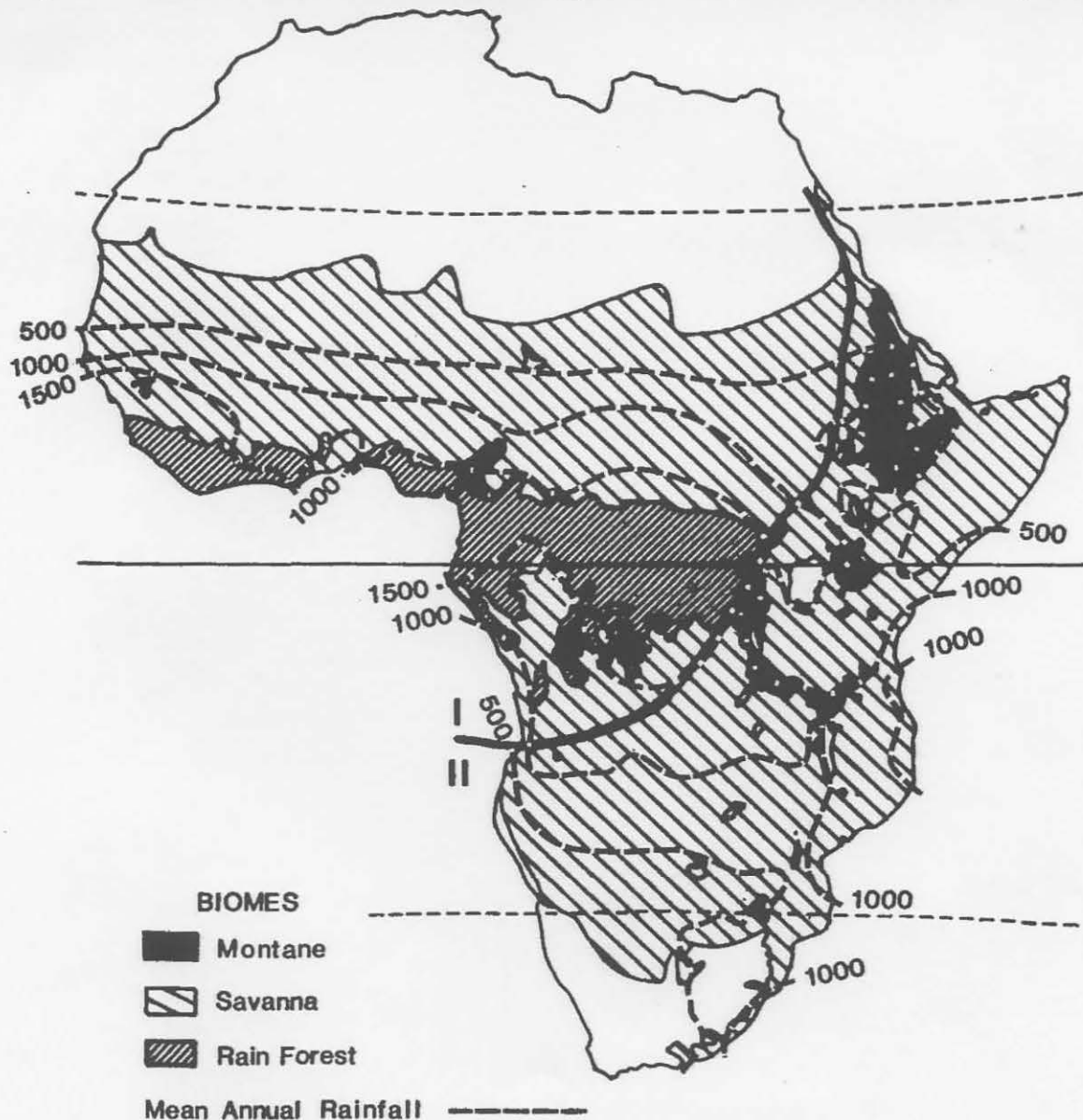


Figure 2. Extent of savanna vegetation in tropical Africa. 1 = savanna biome; 2 = rain forest biome; 3 = montane biome. (Simplified from Aubreville *et al.*, 1958).

time, no information enables to define the relative extension of rainforests and savannas during the Tertiary and Quaternary climatic alternations. Nevertheless, it seems clear that savannas are old, basically natural and have once dominated Africa, compelling forests into isolated refugia. The reverse also occurred and might occur again in the future.

Savannas now cover the large majority of tropical Africa, ca. 15 M km² (Figure 2). They are characterized by the huge heterogeneity of the environment in space and time. Seasonal and interannual variations are certainly among the most important determinants of savanna functioning. One may easily imagine the resulting diversity of physiognomical types of savanna vegetation and the induced variations in the intensity of functional processes. This diversity does not prevent savannas to belong to a valuable and definite entity composed of a number of facies connected the one to the other by a specific link: the grass/tree competitive equilibrium (Walter, 1971). Savanna heterogeneity could thus be the mere expression of the 'behavioural' variations, according to local conditions, of the entity 'savanna'. In any case, spatial and temporal heterogeneity is certainly responsible for some functional characteristics such as the high turnover rates of organic matter and nutrients in plants (often ca. 0.5 in savannas vs. ca. 0.03 in rain forests); this heterogeneity may account for the rapid and innovative changes in animal and plant composition (Bourlière and Hadley, 1983) and finally might be essential to savanna maintaining or stability (Walker, 1981).

PHYSICAL DETERMINANTS

Climate and Fire

African savannas thrive in the seasonal dry-wet zones with summer (hot season) rains and winter (low sun) droughts. 'In truth, no single climatic boundary can adequately discriminate components of vegetation continua' (Nix, 1983): savannas (edaphic or not) do exist within the rainforest biome experiencing low seasonality (if any), frost is a regular phenomenon in the arid savannas of the high plateaus of southern Africa. Neither total rainfall nor rainfall seasonality may provide a good discriminant of savanna types. However, savanna ecosystems functioning clearly depend on the rainfall during the growing season and chiefly on the duration and severity of the dry season. Temperature regime is also of little help. Despite what could be expected from the low temperature in southern Africa the dominance of C4 grasses in savannas is so a marked feature that it was taken by Huntley as an essential diagnostic criterion of the very concept of savanna (Huntley, 1982); C3 grasses, when present, seem restricted to humid sciophilous conditions. Even when using more complex parameters, bioclimatic systems cannot accurately account for the distribution of African savannas (Schulze and McGee, 1978; Sanford, 1982a; White, 1983). However, for practical purposes, three schematic bioclimatic zones may be distinguished. They roughly correspond to three broad savanna types merging into each other according to local conditions (Figure 3).

- Guineo-Congolian or humid zone:
 - Precipitation (P) > 1000mm, dry months (d.m.) < 2, P/ETP > 0.7.
 - Peri — and intraforest savannas. The dense and high grass layer is dominated by scattered trees; grass production is high and annual burnings are severe; no large herbivores are found; soil fauna is very active and dominated by earthworms; traditional utilization by man is light: neither agriculture (if not in forest fringes), nor cattle breeding.
- Sudano-Zambezian or mesic zone:
 - 500 < P < 1200, 2 < d.m. < 8, 0.2 < P/ETP < 0.7.
 - 'Typical savannas'. Competition between grasses and trees is regulated by soil water conditions; grass production is limited by water availability but annual burnings may be severe according to drought; large herbivores exist and soil fauna is characterized by the earthworm/termite balance; traditional intense shifting cultivation is complemented with some cattle breeding.
- Sahelo-Oriental or arid zone (with southern homologue):
 - P < 600mm, d.m. > 8, P/ETP < 0.25.
 - Arid savannas. Vegetation types are overwhelmingly controlled by soil types; burnings are absent or accidental; large primary consumers do exist and soil fauna is dominated by termites; extensive cattle breeding is dominant over complementary light and fixed cultivation.

Grass fires are so intimately associated with savannas that these are often considered as fire-climaxes (Gillon, 1983). Ancient natural fires are attested by Tertiary carbonized cuticles. If their effects on flora and vegetation are difficult to assess, they certainly started the evolution achieved by man-made fires (as old as 50,000 years at least), contributing to the present physiognomic features of the African dry Tropics. Lightning-initiated or man-made, fire is a phenomenon as natural (for definition see Noble *et al.*, 1979) as climate is and present day savannas are the result of a yearly combined drought-fire cycle, in which fire merely amplifies and/or sharpens drought effects. Fire has extremely variable effects from one point to another, from one year to another. It amplifies the local environmental variability, is an added factor of heterogeneity in the short term. Over several years, fire occurs at last wherever an herbaceous cover exists and results in constant effects on all sites it goes through. In the long term, it is a factor of homogeneity. All other conditions equal, fire rather tends to maintain the local landscape. This contention is also borne out by Sanford (1982b) who states that 'annual

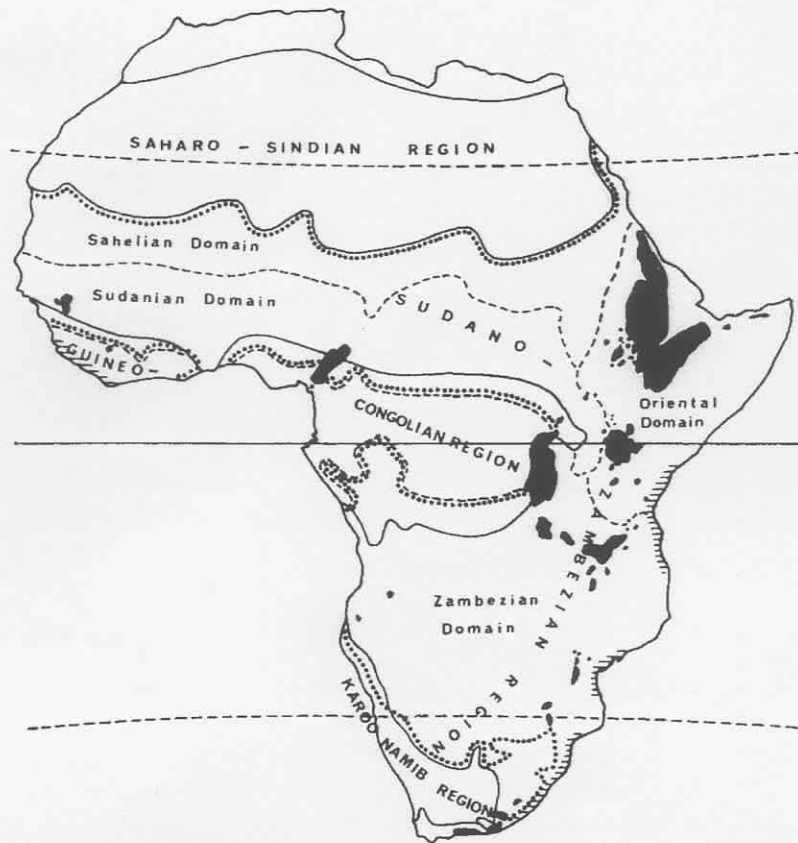


Figure 3. Broad bioclimatic zones and savanna types in tropical Africa. (from Menaut, 1983).

burning acts as a stabilizing environmental pressure, bringing about a less variable, more constant over time vegetation than occurs with fire protection'.

Fire is the more essential to savanna maintenance the more humid the climate. Moist savannas, heavily loaded with herbaceous fuel, experience fierce fires initiating a sharp boundary with the neighbouring forest and preventing fire-susceptible species to settle. In arid savannas, fires occur very rarely; the herbaceous cover is often too poor to carry a fire front (droughty conditions and livestock consumption) and burning is by all means fought by herdsman. The standing dead cover disappearing very rapidly by consumption and trampling by cattle, it is difficult to assume what would occur if fire replaced cattle. Would the annuals/perennials balance of the herbaceous cover change, as often suspected?

Soils

Mainly formed a large sub-horizontal surfaces on which alteration processes have continuously occurred during millions of years, Africa brings up all conditions of a pedogenesis led to its ultimate term. In humid conditions, allitization of crystalline rocks tends to eliminate alkalis, lime, magnesia and even silica and results in the formation of laterite. In these conditions, alteration correspond to an intense hydrolysis leading to a soil with a chemical composition totally different from that of the mother rock. In drier conditions, alteration (kaolinization) is less severe (lower leaching of silica) and may even be reduced to mechanic desagregation in arid conditions.

Parent material diversity is thus not directly reflected by soil types. Geomorphology and climate aggressivity are the predominant features determining the degree of alteration of the rocky substrate and the degree of leaching. Both are the major agents in the evolution of clays and in soil differentiation.

Soil Regions

Three broad soil types may be recognized in the savanna biome (Figure 4).

1. *Ferralsols* represent the final stage of ferralitic weathering (low absorbing complex, often highly desaturated, very low mineral reserves, limited fertility). They generally occur under heavy rainfall climates. They bear grassy patches within the rain forest biome and some Miombo forests (central and southern Africa).
2. *Luvissols* are found in the fersialitic pedoclimatic zone covered with tree savannas and woodlands (most of the Sudano-Zambezan region). *Ferric luvissols* (humid conditions) are highly weathered: low exchange capacity, good saturation in cations, organic matter poverty, low fertility). *Chromic luvissols* occur in drier conditions: they are well provided with bases and would be fertile were not their relative poverty in organic matter and phosphorus. *Acrisols* belong to the same pedoclimatic zone but are even more weathered than the ferric luvissols.

3. *Arenosols* are sandy soils, poor in organic matter, exchangeable bases and phosphorus. Often developed from ancient consolidated and fairly rubified dunes, they constitute most of the Sahelian zone and the Kalahari system. *Ferralic arenosols* occur in perhumid conditions and are even poorer.

Particular soil types occur according to local conditions. Among the most important, *vertisols* often develop on basic, low leached rocks. They occur in regions experiencing a marked dry season and are absent from the humid ferralitic zone. They occur in any savanna zone and many African valleys are covered with vertisols. They are rich, often alkaline soils but heavy and with a low permeability. They may be covered with characteristic woodlands (e.g. *Acacia seyal* pure stands) or with grass savannas providing good pasture.

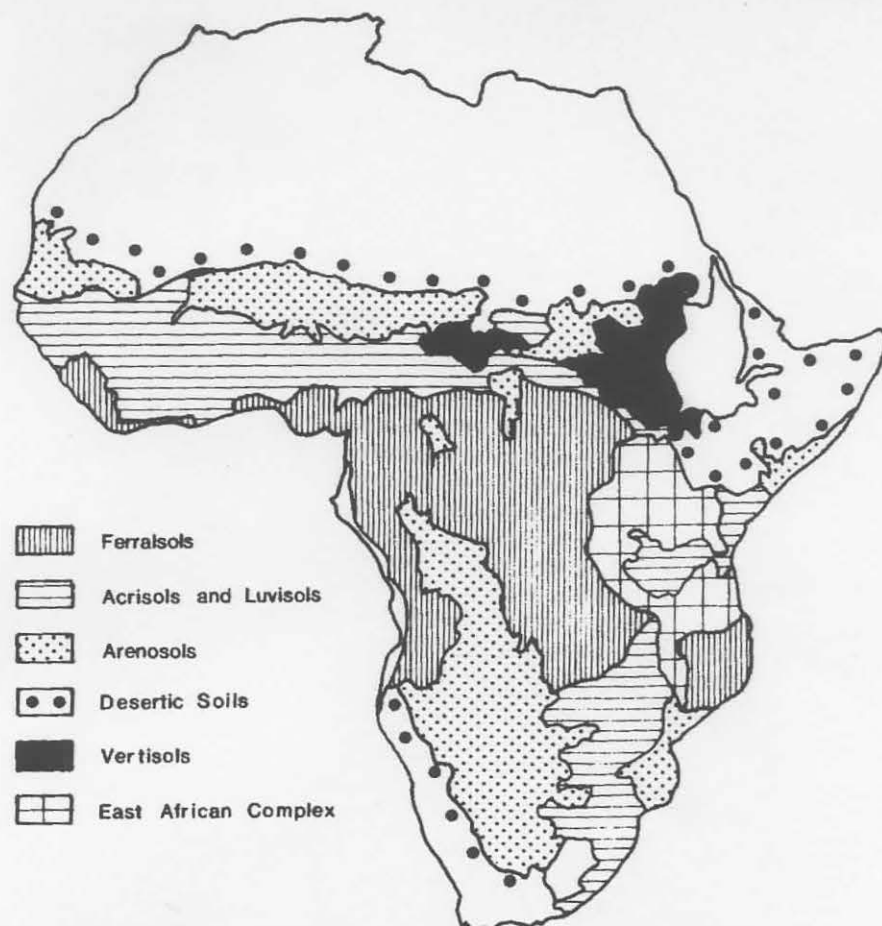


Figure 4. Broad soil regions of tropical Africa (simplified from FAO-UNESCO, 1977).

Catena Effect

These broad soil types indeed conceal a much more complex distribution at regional scale where catena effects induce a variety of soil types along short transects (Milne, 1935). These effects are of such ecological importance that catenary sequences of soil and vegetation constitute one of the most significant units of comparison. Examples are given by Morison *et al.*, (1948) in East Africa, by Latham and Dugerdil (1970) in West Africa and by Tinley (1977, 1979) in southern Africa.

In savannas, plateau soils usually have upper horizons composed of sandy loams dominating a pea-iron horizon, its depth directly compels the mosaic patterns of soil and vegetation. In dry areas, ironpans generally lie on the soil surface, erosion often leading to flat-topped outliers covered with a loose scrub. Along the slope, the ironstone softens and even disappears. Low-lying soils are generally characterized by an enrichment in altered clays leached from the upper levels. Deep compact grey clays often form an impermeable horizon so that downslope soils are often flooded in the rainy season. In humid conditions (Guineo-Congolian zones), vertical movements of the water table activate leaching and alteration of clays (Raunet, 1982). Clayey horizons may still occur down the profile but they often disappear, giving place to deep, leached, almost pure sands, with rusty mottling attesting their hydromorphism in the rainy season.

Physico-chemical characteristics

Broad characteristics of the main soil types according to an indicative rainfall gradient are given in Figure 5. Soils tend to be the more acid the more humid the climate and organic matter contents rapidly decrease from the humid regions to arid savannas (Charreau, 1974). Comparable trends have been observed for nitrogen and total phosphorus (Roose, 1980). These trends have been quantified by Kadeba (1978) along the latitudinal climatic gradient occurring in Nigeria (from 1800 to 500 mm annual rainfall). Per cent contents of carbon and

nitrogen in the soil are linearly correlated to mean annual rainfall and even better to the number of rainy days (L): $\%C = 0.0204 L - 0.912$ and $\%N = 0.00121 L - 0.043$. Total exchangeable bases and organic matter follow opposite trends. TEB markedly increase from the highly altered and leached ferralsols (and acrisols) of humid regions to the less evolved and less leached luvisols of drier areas. However, dryness increasing, arenosols and regosols display lower TEB contents. In southern Africa where different soil types may occur in mosaic within small areas, arid/eutrophic soils have been opposed to moist/dystrophic soils (Huntley, 1982). Relationship between soil trophic level (nutrient status) and geomorphological situation has been pointed out by Bell (1982): ancient elevated granitic shields are poorer in nutrients than more recent sedimentary and alluvial depressions. Though real in the principle, such generalization is of rather low ecological interest. Apart from some particular situations (e.g. volcanic material), available values display too wide ranges. It must also be noted that low alluvial detritic grounds, when not closed (endoreic), may themselves be severely leached and may not display better nutrient status than higher grounds.

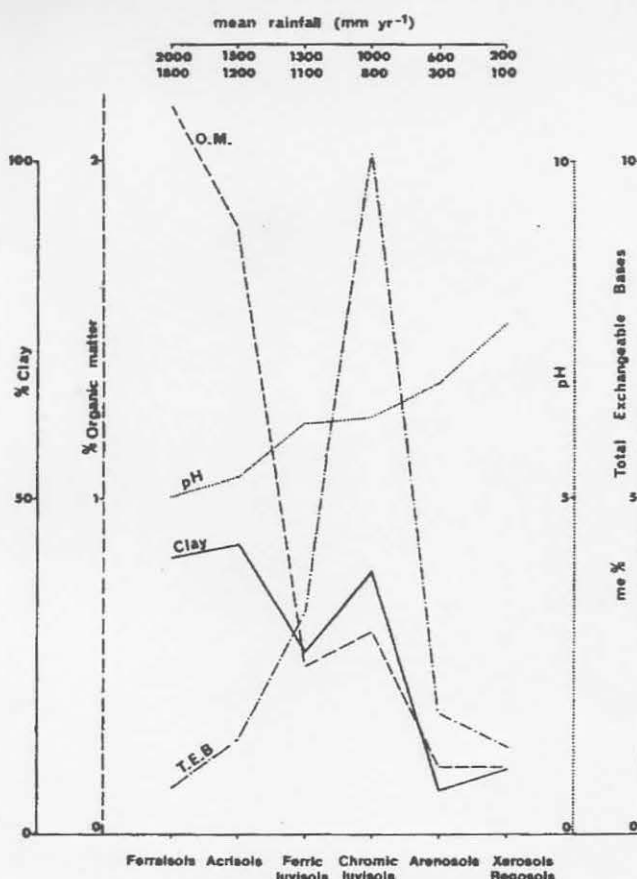


Figure 5. Regional trends of soil physico-chemical characteristics in tropical Africa (data from FAO-UNESCO, 1977).

Hydric regimes are certainly major determinants of savanna functioning. Correlated with rainfall, physiography, vegetation and soil types, it is undoubtedly a highly variable parameter; its frequent and drastic changes in space and time have dramatic effects on living organisms and nutrient transformation and availability. As shown by Lavelle (1978), fifteen days with low rainfall — even in the rainy season — may dry out a soil which was previously saturated. Vegetation types have a crucial effect on soil water regimes: trees, still pumping water in the dry season, tend to dry out the soil. This effect is particularly clear in the 20–40 cm depth soil layer where tree roots are more abundant; if dense enough, they may prevent water saturation. This explains how the removal of woody species (e.g. bush-clearing or death during a temporary dry spell) may induce soil waterlogging and the establishment of a grassland under which high field capacity can only be attained and maintained (Tinley, 1971). Conversely, drier periods in usually drowned soils may favour the establishment of a woody cover which will, when usual rainy conditions come back, pump the soil of excessive waterlogging, preventing the re-establishment of the initial grassland. Long spells of rainfall modification may thus induce self-preserving plant formations. Successional dynamics across catenary sequences has been described by Tinley (1979, 1982). On the other hand, the shade effect of tree canopy may protect the superficial horizons from drying, which may effect the composition of the herb layer (César and Menaut, 1974) and protect the activity of the litter and soil fauna (Lavelle, 1978).

Seasonal variations in thermic regimes deeply affect soil functioning: the soil is bare at the end of the dry season when air temperature is maximum and water supply is most critical. In arid savannas, the herbaceous

layer has disappeared through weathering and trampling. In humid savannas where bush fires have destroyed the grass layer, the soil remains covered with dark ashes. In both cases, soil heating is extreme (over 50°C in the upper most centimeters) and the resulting effects are experienced by soil fauna even in the deeper horizons (Athias, 1974; Lavelle, 1978).

Main Soil Systems.

Broad soil systems may be distinguished according to their nutrient status, organic reserves, water and temperature regimes.

- 1) *Arid soils* have a relatively high exchangeable base content if not too sandy and have a low humic stock; they suffer from long severe heating and from long water deficits.
- 2) *Moist soils* have a lower exchangeable bases content but a higher humic stock; they only suffer from heating during a short period and are well watered.

In African lowlands, these two extremes are respectively characteristic of the Sahel zone and of the Guinea zone; all intermediate situations occur according to rainfall and temperature gradients (clear zonation).

In African highlands, cooler temperatures may induce changes in soil processes and soil communities metabolism. Zonal distribution of arid and moist broad soil systems also occur in southern Africa; they do not correspond to the arid/eutrophic and moist/dystrophic mosaic observed at local scale.

Distribution of plant communities : determinants

One generally agrees that climate (i.e. the occurrence of a marked dry season) and/or fire account for the origin of savannas, but the determinants of the maintenance and evolution of the different vegetation types encountered within the savanna biome are still debated. Any structural category of savanna occurring in any climatic region and on very diverse soil types, simplistic generalizations are unsecure as shown in Menaut (1983) and White (1983).

However, relationships between vegetation types and geomorphology have been pointed out by Cole (1963, 1982). The savanna biome extends over contrasted land forms as opposed to what occurs in forest regions. These land forms generally induce specific savanna vegetation types.

Savanna woodlands are associated with old planation laterized surfaces. They also extend onto younger areas of exposed bedrock or redistributed laterite. Tree/shrub savannas are usually found on younger and lower planation surfaces such as the detritic sandplains bordering lateritic plateaus. Savanna grasslands are restricted to laterized hardpans mantled with thin soils and to sandy or heavy clayey depressions; in both cases, seasonally alternating waterlogging and drought are unfavourable to tree growth. When drainage is improved, grasslands generally give way to tree savannas.

The relationships between soil characteristics and the distribution of plant formations have often been discussed but the work of pioneers such as Michelmore (1939), Walter (1939) and Morison *et al.* (1948) has regrettably initiated few further researches. They have shown how the distribution of savanna plant communities is determined by the reaction to local conditions of each of their both components, grasses and trees. This close association is unique in natural plant formations of the world and Walter has provided masterly ecophysiological hypotheses to explain how soil moisture availability could compel this 'competitive equilibrium'. The description and interpretation of the distribution of savanna types in central and southern Africa provided by Walter (1971) followed by Tinley (1982) proves the approach to be extremely fruitful. Recent advances in savanna plant ecophysiology and ecological modelling have led Walker (Walker, 1980, 1981; Walker *et al.* 1981; Walker and Noy-Meir, 1982) to propose enlightening models on this equilibrium and savanna dynamics (Figure 6). Walter's hypotheses and Walker's models are partly based on disputable assumptions but they provide at last a general tool for the comparison of the different situations observed in African savanna plant communities.

Soil nutrients have often been put forward as a major determinant of savanna occurrence and savanna typification. This is questioned by Tinley (1982) who notes that the most infertile soils support a variety of ecosystems from pure grasslands to evergreen forests. Other authors (e.g. Cole, 1982) think that the soil nutrient status may influence the composition of the vegetation within a given savanna type but is not responsible for this particular structural type. A number of authors thought that some grass savannas were bound to soils of extreme poverty (e.g. Robyns, 1936; Duvigneaud, 1952). Bell (1982) disputes this view, arguing that 'for a given rainfall, plant biomass tends to be lower in conditions of higher soil nutrient availability'. For Bell, plant biomass represents tree density (from rainforest to grassland) and soil nutrient status means Cation Exchange Capacity and phosphorus content; conclusions could be different when considering organic matter and nitrogen. However, nutrients are not only mere soil characteristics but are also a function of the inputs originating from the organic and element cycling of the local vegetation. We shall see that the modalities of nutrient cycling and absorption by roots could much more determine vegetation types than the absolute amount of such and such nutrient.

It is thus extremely difficult to distinguish the actual effect of a single or combined factor, both in the short and in the long term and at the different levels of integration of savanna biotic systems. Though oversimplified, the following assumptions may be proposed:

- Soil moisture regime (a combination of climate, soil type and physiographic position) seems, in the state of our present knowledge, to be the overriding determinant of savanna structure, i.e. the relative abundance of herbaceous and woody species. Though soil moisture be in return influenced by vegetation and soil organic matter, it is predominantly dependent on abiotic environmental factors on which biotic features only have a slight or localized influence.
- Soil nutrients, herbivory and fire keep up complex, close and reciprocal relationships with vegetation and also with all the biotic components involved in matter cycling. Any change in these 'factors' tends to be buffered and regulated within the whole system. However, a slight but long-lasting variation in one of them might induce a long term slow evolution of the system, more at species composition level (mostly within the herb layer) than at a structural level (herb/tree balance). The question arises whether this evolution leads to long term ecosystem cycles or not. This question also worths for drastic changes in these factors like fire protection, elephant overbrowsing, removal of grazers through rinderpest; these changes may of course induce rapid variations in vegetation structure which might disappear in the long term (aspect of the resilience of savannas). It is only when acting in synergy with soil moisture that a modification in one of these factors may lead the system to a threshold beyond which it falls into another domain.

Presently, one may accept that soil nutrient status plays its major role in influencing species composition of the grass layer and the biotic processes of its own recycling, that fire tends to maintain the prevailing situation and that 'the evidence currently available is too meagre to assess fully the influence of large herbivores on savanna structure' in the long term as argued by Cumming (1982). Soil moisture balance is the most documented and argued determinant; it overrides all other properties or influences their effects.

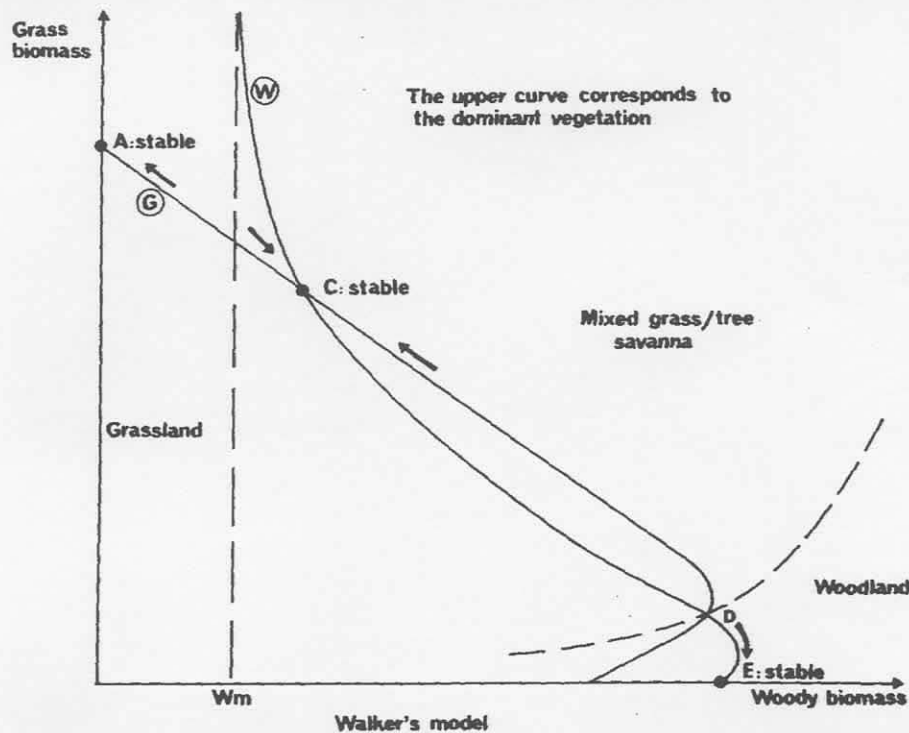


Figure 6. Combined dynamics of grasses and trees in African savannas (adapted from Walker *et al.*, 1981).

SOIL FUNCTIONING

The distinction between arid and moist savannas can be based on:

- water availability;
- nutrient status of the soil;
- biological processes of nutrient release and cycling.

These biological processes, involving the whole litter and soil fauna, are dominated by microbial life. In savannas, this microbial life is mainly regulated by earthworm and termite activities, the whole system depending primarily on the moisture status of the soil.

Earthworms

No earthworms are found below ca. 800 mm annual rainfall. Several categories based on their feeding behaviour may be distinguished (Lavelle, 1983):

- Epigeic: feed on litter and live in litter;

- Anecic: feed on litter, live in the soil;
- Oligohumic: feed on soils poor in organic matter (deeper horizons);
- Mesohumic: feed on soils with medium richness in organic matter (upper horizons);
- Polyhumic: feed on soils rich in organic matter, i.e. in localized places such as dead roots.

The proportion of epigeic and anecic earthworms (litter feeders) increases with drought stress in the soil — along a catena as well as along a climatic gradient. Correlatively, earthworms living in the deeper horizons disappear and the specialized oligohumic worms only remain in the soil (Figure 7).

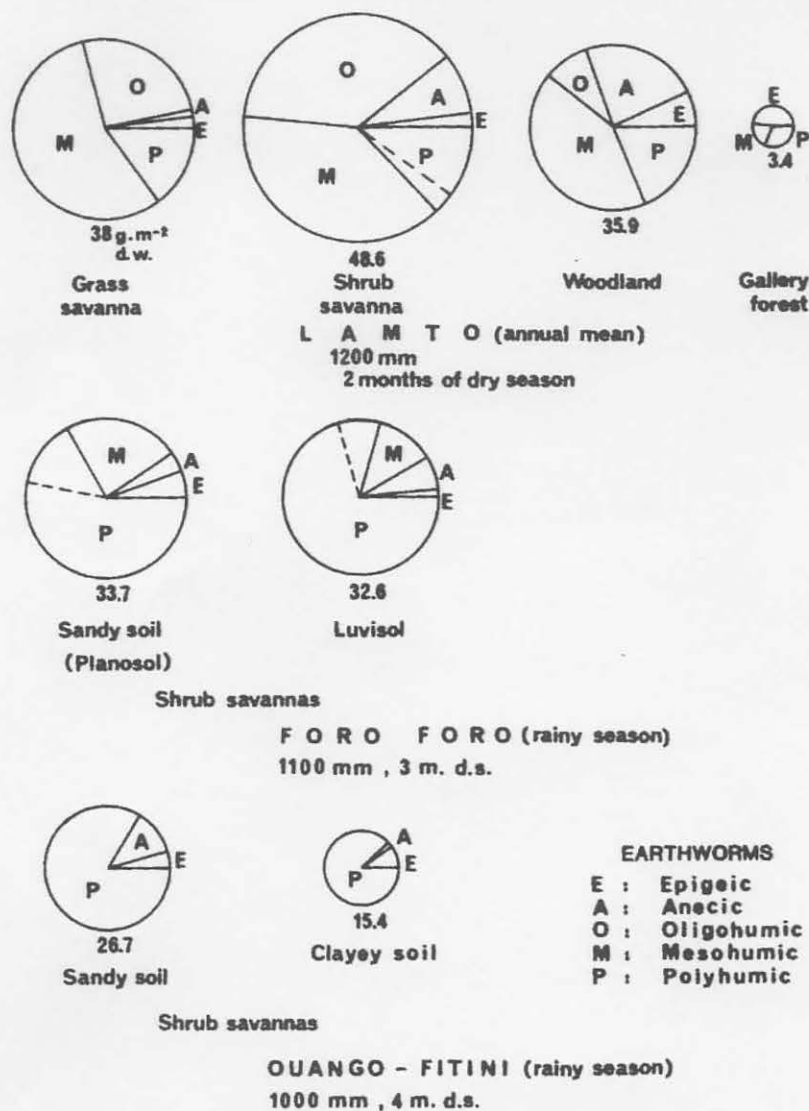


Figure 7. Variation of earthworm populations according to water availability in savannas of Ivory Coast.

The role of litter feeding epigeic and anecic earthworms is rather unimportant, specially in moist savannas. These worms are not numerous and thus have a low effect on total litter decomposition as compared to termites. However, they incorporate some litter into the soil and slightly participate in the accumulation of soil organic matter.

Endogeic earthworms are very active soil mixers. In moist soils, adults daily ingest at least three times their own weight or dry soil and up to thirty times for young worms. As a result, earthworm populations ingest huge amount of soil, above 1000 t ha⁻¹ yr⁻¹ in moist savannas for example (Lavelle, 1978). 25 t only of ingested soil are deposited on the soil surface, the rest remains, in a transformed state, within the soil. This ingested soil contains 20-30% of the total humic reserves of the soil. However, worm activity is maximum in the upper horizons (between 0-10 cm deep) where up to 70% of the soil organic matter is processed through earthworms (Figure 8). This organic matter is partly transformed inside the worm guts where an important input of mucopolysaccharides is added. Microbial activity is increased, in fact started, and may last within a worm cast for around a month. The density of earthworm populations and the duration of their activity along the year — depending on soil water status — have a major effect on microbial activity and consequently on available nutrients (Lavelle *et al.*, 1983a).

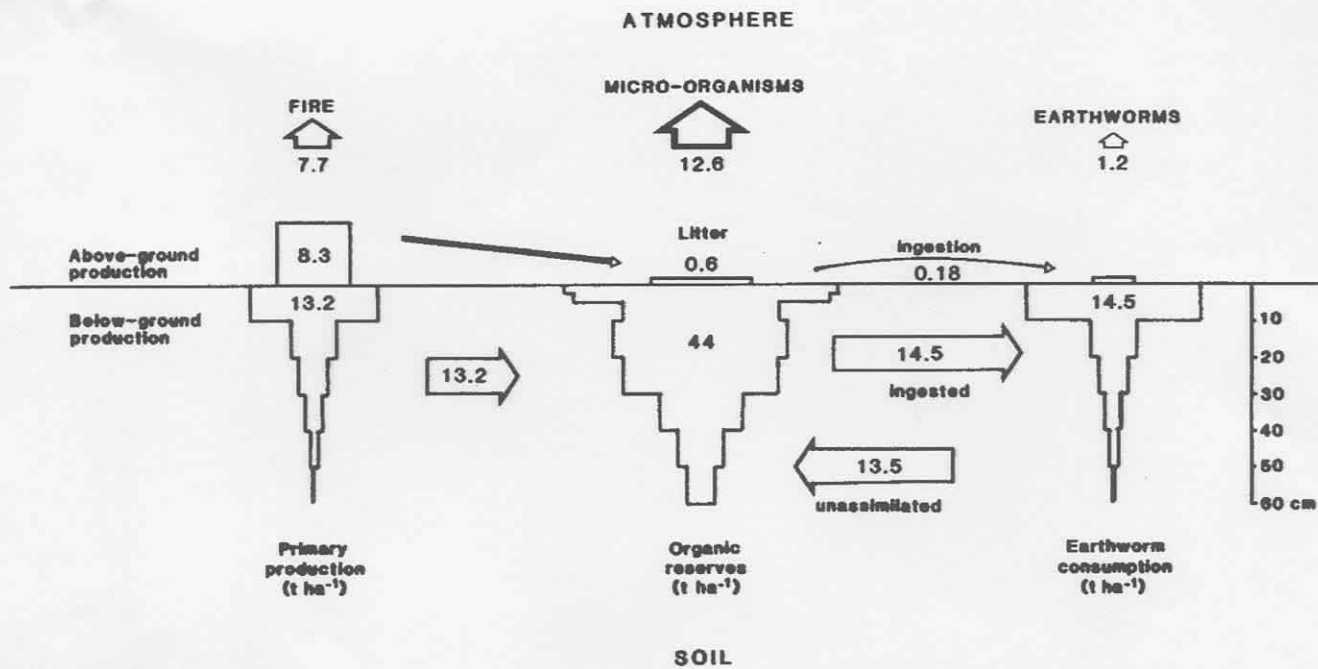


Figure 8. Role of earthworms in the decomposition processes of organic matter in a moist savanna (from Lavelle, 1978).

Termites

As compared to earthworms, termites exist throughout the savanna biome and their importance on nutrient cycling increases under dry climates where grass and litter eaters are particularly numerous (Lepage, 1974) (Figure 9).

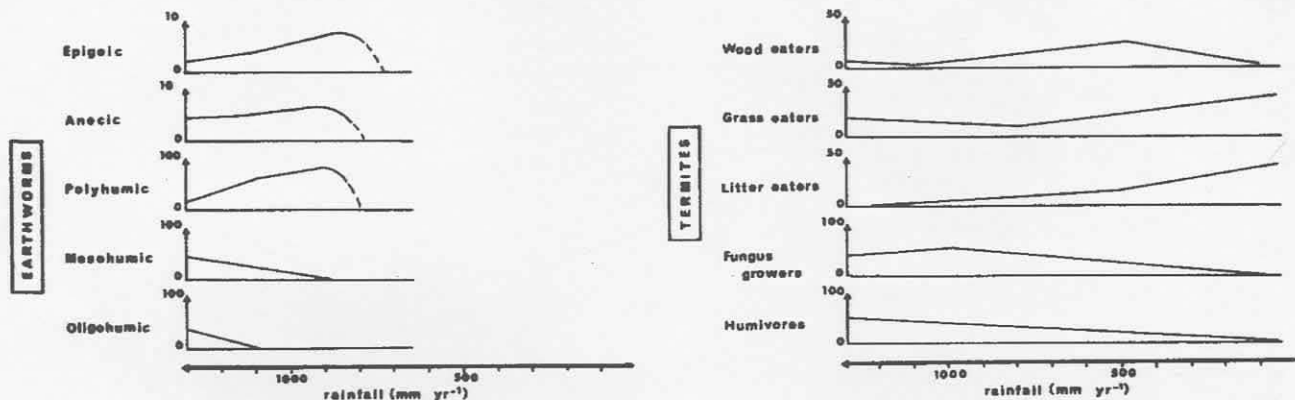


Figure 9. Variation of earthworm and termite populations (percent of the total number of species) in relation to mean annual rainfall.

The role of termite-mounds can be radically opposite, depending on rainfall regime: termite activity tends to lower productivity when water availability is low and to increase productivity when water availability is high (Figure 10). This is observed along a climatic gradient as well as one site experiencing variable rainfall. The average role of termitaria may be easily exemplified in mesic environments, i.e. in most of the Sudano-Zambeian region (Figure 10).

- The enrichment of the upper horizons of the soil in finer elements tends to increase drought stresses in these horizons. Grass production is thus lowered. The decreased competition with grasses and the increase of water remaining in the deeper horizons favour the development of trees.
- Trees take also benefit from the enrichment of the soil in nutrients which are slowly released. Their development enhances shading above-ground and water absorption below-ground: grass production is impeded. Tree leaf and wood litter productions increase and feed more termites. The systems are stabilized in a woodland, the density of which depends on soil water maximum availability for trees.

The activities of termites constitute a major pedological factor (Lee and Wood, 1971; Montgomery and Askew, 1983) though this is sometimes questioned (Pomeroy, 1976, 1983). It has been a long time since

woodland soils have been considered to be, at least partly, termite formed (Nye, 1955; Watson, 1974; Roose, 1976). Termite mounds play an important role in the conservation of the organic matter. Litter consumption by termites is generally ca. 30% of litter biomass (Josens, 1983) but may reach almost 70% in some Sudanian woodlands (Ohiagu and Wood, 1979). Many authors (e.g. Watson, 1975) have shown that carbon, nitrogen and exchangeable bases are concentrated in termitaria; nutrients are afterwards slowly released into the soil.

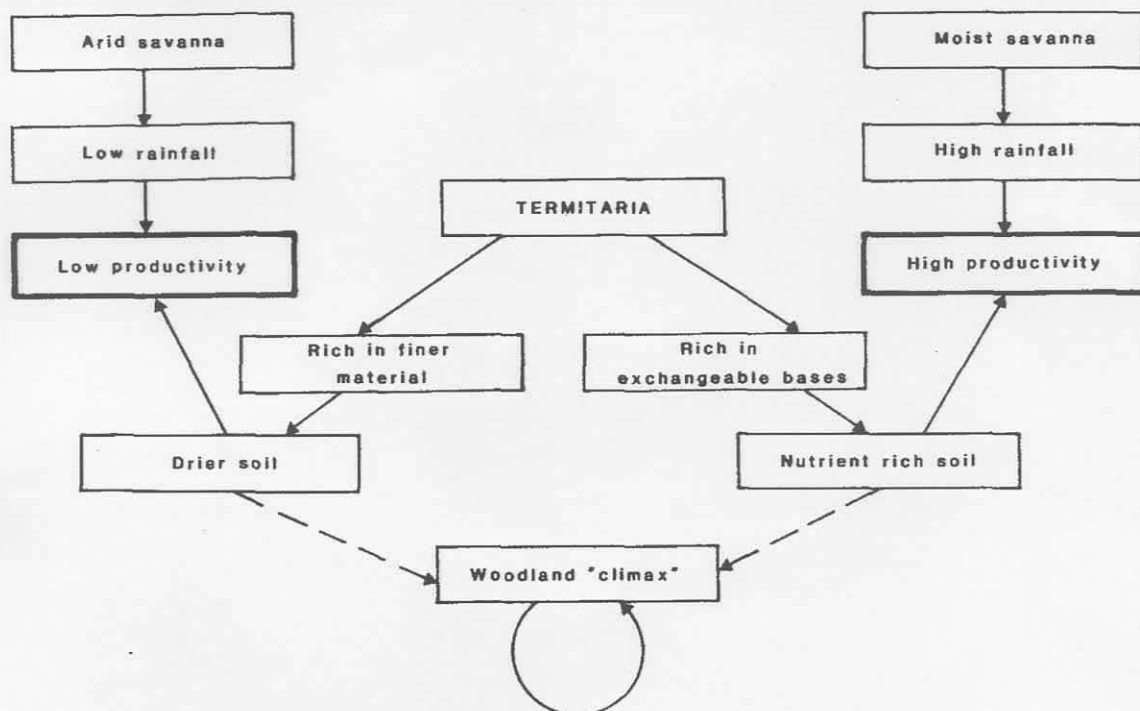


Figure 10a. Influence of termite-mounds on primary production in relation to rainfall.

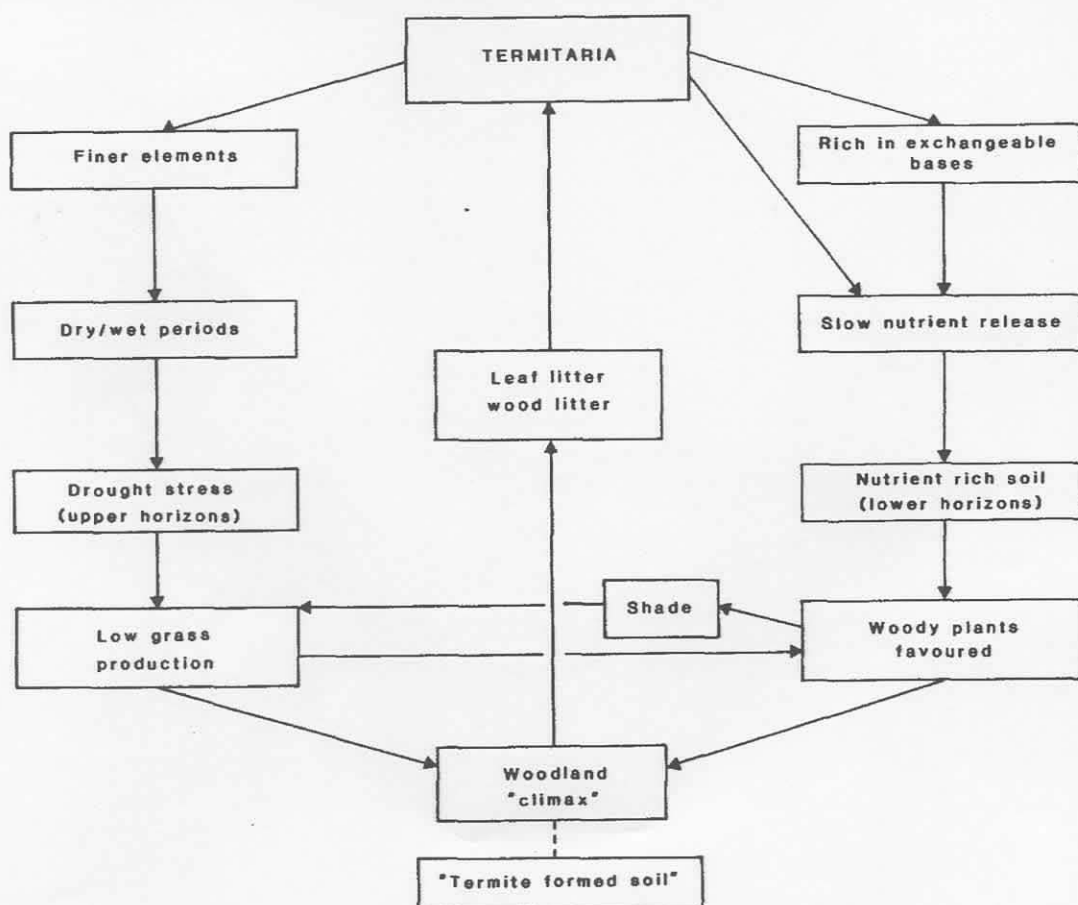


Figure 10b. The termitaria-woodland equilibrium of mesic savannas.

It is sometimes argued that this organic matter accumulation may, in some cases, be deleterious (competitive storage) to the whole system (e.g. Ohiagu, 1982). Arid savannas apart, it has to be noted that most of the above-ground organic matter normally would have been destroyed by fire, where not consumed by termites. It is also generally considered that litter plays a light role in soil humus formation, this humus mostly originating from root decomposition. The major role of litter, as far as soil biological processes are concerned, is to release minerals and small carbon molecules (see below). Termites activities modify the spatial and temporal distribution of this release but do not prevent it.

Nutrient release in arid and moist savannas

Dry savannas are characterized by rather simple systems of nutrient release (Figure 11). These systems start rapidly at the onset of the rains and do not always remain active during the whole rainy season (Bernhard-

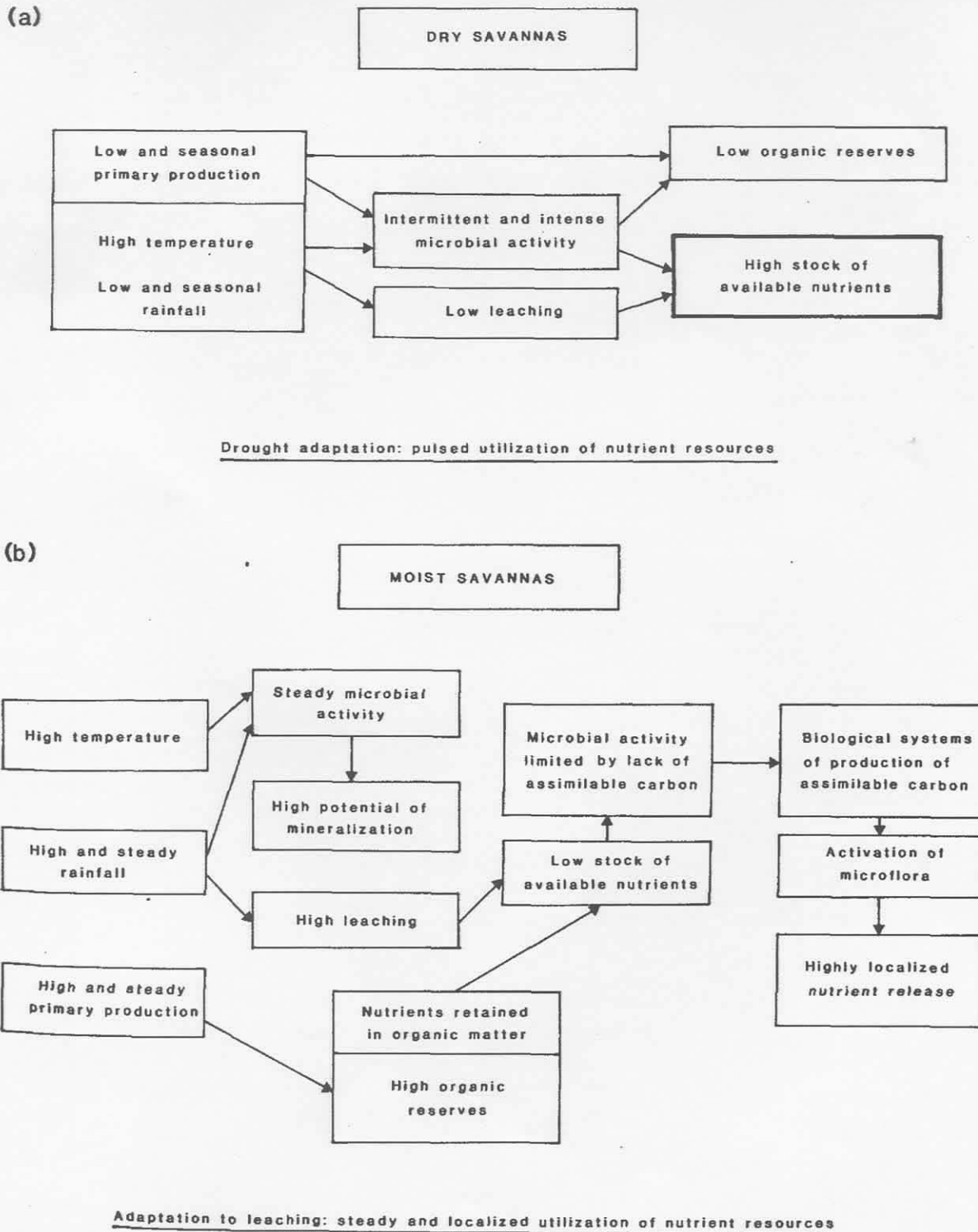


Figure 11. Nutrient release and organic matter accumulation in (a) dry savannas, (b) moist savannas.

Reversat, 1982). Litter and rhizosphere systems are very comparable in intensity (depending on the above-ground/below-ground primary production ratio) and duration. Organic reserves are low due to the low primary production by lack of available water (Bille and Poupon, 1972; Sicot and Grouzis, 1981). Nutrients are released during the short but intense microbial activity; a large amount of them are not leached and constitute a relatively high stock of nutrient reserves.

The system of nutrient release is much more complicated in moist savannas (Figure 11). High temperature and rainfall should promote an important steady microbial activity resulting in a high potential of nutrient release. Due to intense and constant possible leaching, conservation mechanisms shall occur. A large part of nutrients is unavailable as stocked in the organic matter (Kadeba, 1982) and is slightly but steadily mineralized throughout the year. This low mineralization within the soil is due to the limited activity of micro-organisms by lack of assimilable carbon. Mineralization also comes from litter percolates since the very beginning of the rainy season; it lasts all year long according to litter production cycle. The rhizosphere system displays a slower start but functions at a higher level; it does not stop completely during the short dry season: some water being still more or less available. It is expected that dew and occult condensations within the soil may play a role at this level.

Arid and moist systems mainly differ by their duration and relative importance of the litter and rhizosphere components (Figure 12). They consequently display, in relation to water availability, different nutrient release regimes; both parameters may determine various types of savanna exemplified by the balance between annuals and perennials (Figure 13).

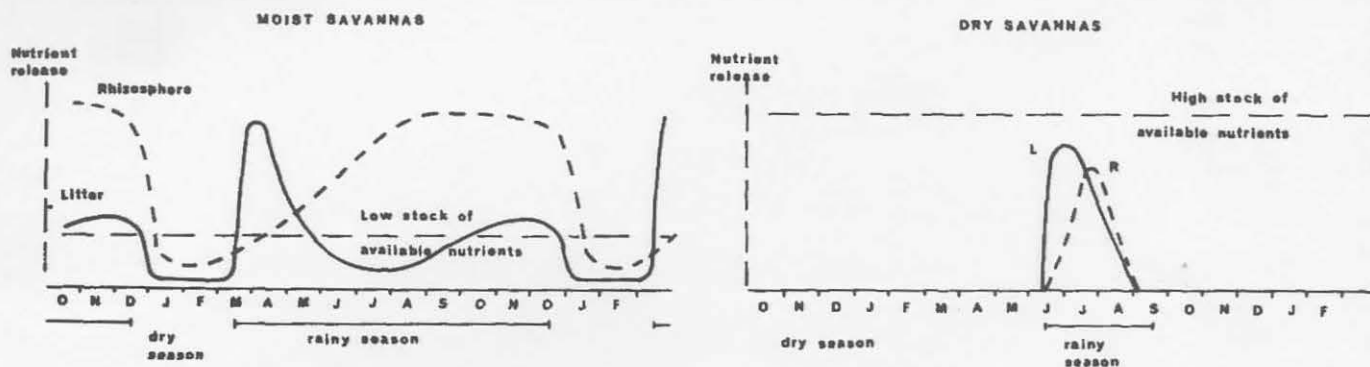


Figure 12. Schematic comparison of the nutrient release systems in dry and moist savannas.

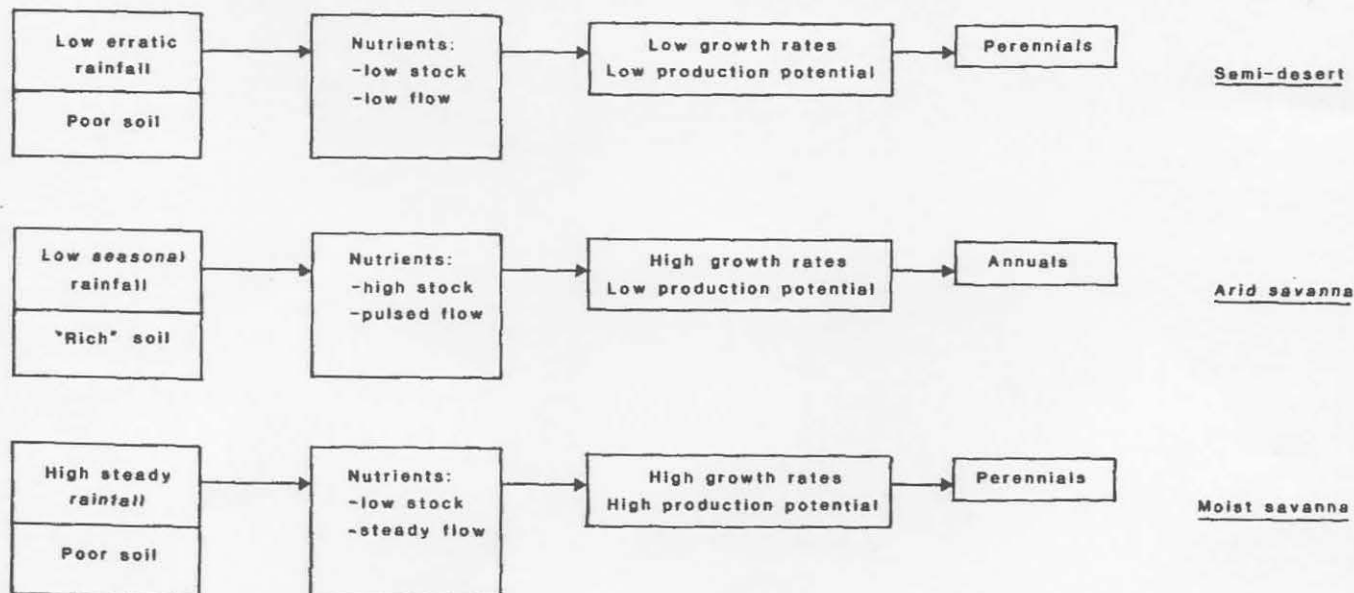


Figure 13. The balance between annuals and perennials according to rainfall and nutrient release.

Semi-desert conditions: the poorness of the soil and the erratic rainfall lead to a low stock of nutrients which are slowly released. This induces the development of perennials, annuals appearing by chance according to the amount of rainfall.

In arid conditions, the high stock of nutrients is rapidly released when rainfall occurs. The short duration of this pulsed flow favours the development of annuals.

In moist conditions, soils are relatively poor but the steadiness of rainfall makes the nutrients more or less constantly available: perennials are favoured.

These broad distinctions point out different types of water and nutrient availability. They particularly show that the modalities in space and time according to which nutrients are released and absorbed by plants are much more ecologically significant than the total amount of nutrients stocked.

SOIL MODEL

Moist system (Figure 14a)

Inputs of organic matter follow two pathways. The first is bound to litter and superficial roots; the second to the bulk of the root system.

Litter system

Little organic matter originating from the above-ground litter participate in the formation of the humic stock as ca. 70% of total above-ground production is consumed and burnt (Menaut and César, 1982). Mineralization is essentially realized by fire and minerals are partially integrated into the soil as soon as the first rains occur (Delmas, 1967).

The epigeic community is composed of micro-organisms and invertebrates that feed on the litter and live in it. This epigeic community directly decomposes a small part of this litter. The anecic community is made of micro-organisms and invertebrates that feed on the litter and draw it into a different decomposition system; it is dominated by termites (foragers or fungus-growers) which bring the litter into their nests.

Due to the accumulation of litter at the end of the rainy season and to fire occurring rapidly afterwards, nutrient release by this system is highly seasonal. A flush of available nutrients (minerals and hydrosoluble organic matter) is produced at the beginning of the growing season. Afterwards, the system remains more or less active; litter slowly accumulates and is partially decomposed and leached. Termite activity tends to lengthen the functioning of the above-ground system. Nutrients stocked in termite-mounds are slowly released after the death of the colony throughout the rainy period.

Root system

Roots, when dead, are directly decomposed by micro-organisms. Fungi seem to play a major role at this stage whereas the activity of soil fauna is very descreet. There are no rhizophages and roots seem to be a poor nutritive resource: experiments showed that earthworms fed on litter had a far greater growth than those fed on roots (Lavelle *et al.*, 1980). It can also be advanced that fractioning and mixing of roots with the soil is of no use when considering nutrient release, as we shall see that these roots are directly bound to a dense muff of associated microflora. The high production of roots in moist savannas contributes to create a high humic stock (Menaut and César, 1979). Few nutrients have been released at this stage and most of them remain concentrated within the organic reserves of the soil.

Humic stock

The humic stock is made of a mixture of fulvic, brown humic and grey humic acids which represent different stages of molecular condensation. In moist savannas, grey humic acids which are the most complex and stable (over 100 years of life span) may represent up to 35% of the total humic stock (Lavelle and Schaefer, 1974). Most of the soil nutrients are thus concentrated in unaccessible organic compounds. This might be considered as a mechanism preventing losses by leaching if these nutrients were immediately mineralized (Bate, 1981).

Though the nutritive value of the soil organic matter varies along the year, the lack of a minimum quantity of assimilable carbon (ca. 0.2 per mil in Lamto savannas) make this humic stock a not very accessible food resource for soil organisms. As the total amount of organic matter does not vary significantly along the year and between years, regulatory mechanisms have to occur.

Biological activation

The release of nutrients contained in the humic stock is made possible by systems of biological activation which are able to produce assimilable carbon in localized sites. This assimilable carbon stimulates the activity of the microflora which then becomes able to mineralize complex molecules.

Only nitrogen fixers have a constant need of energy through assimilable carbon. For other bacteria, the assimilable carbon is used to activate the population and enable them to attack complex molecules and split them into simpler ones. Food is thus provided to the bulk of the microorganisms consuming organic matter; otherwise, they remain most of the time in energetic starvation (Abbadie, 1983). This priming effect (or starter effect) is not long lasting; for instance, it lasts only one month among bacteria activated by earthworm mucus.

The assimilable carbon comes in small quantities from litter and dead roots leachates. It is mainly provided by root exsudates and earthworm cutaneous and intestinal mucus. Young (1976) estimated that roots could exsude ca. 150 kg ha⁻¹ yr⁻¹ of organic carbon. This roughly corresponds to 1.5% of root production. In temperate countries, root exsudates may reach 10% of root production. This point has to be thoroughly studied in tropical savannas but it may be assumed that root exsudates may reach high values.

Production of mucus by earthworms represents ca. 16% of the dry weight of ingested soil by geophages: knowing that earthworms may ingest $1000 \text{ t ha}^{-1} \text{ yr}^{-1}$, this leads to ca. $160 \text{ t ha}^{-1} \text{ yr}^{-1}$ of mucus production (Lavelle *et al.*, 1983b). This amount mucus is not released into the soil. It is in most part reabsorbed by the earthworm at the end of the transit. However, during this transit, the soil has been activated and may still be 20% richer in assimilable carbon when rejected by the earthworm.

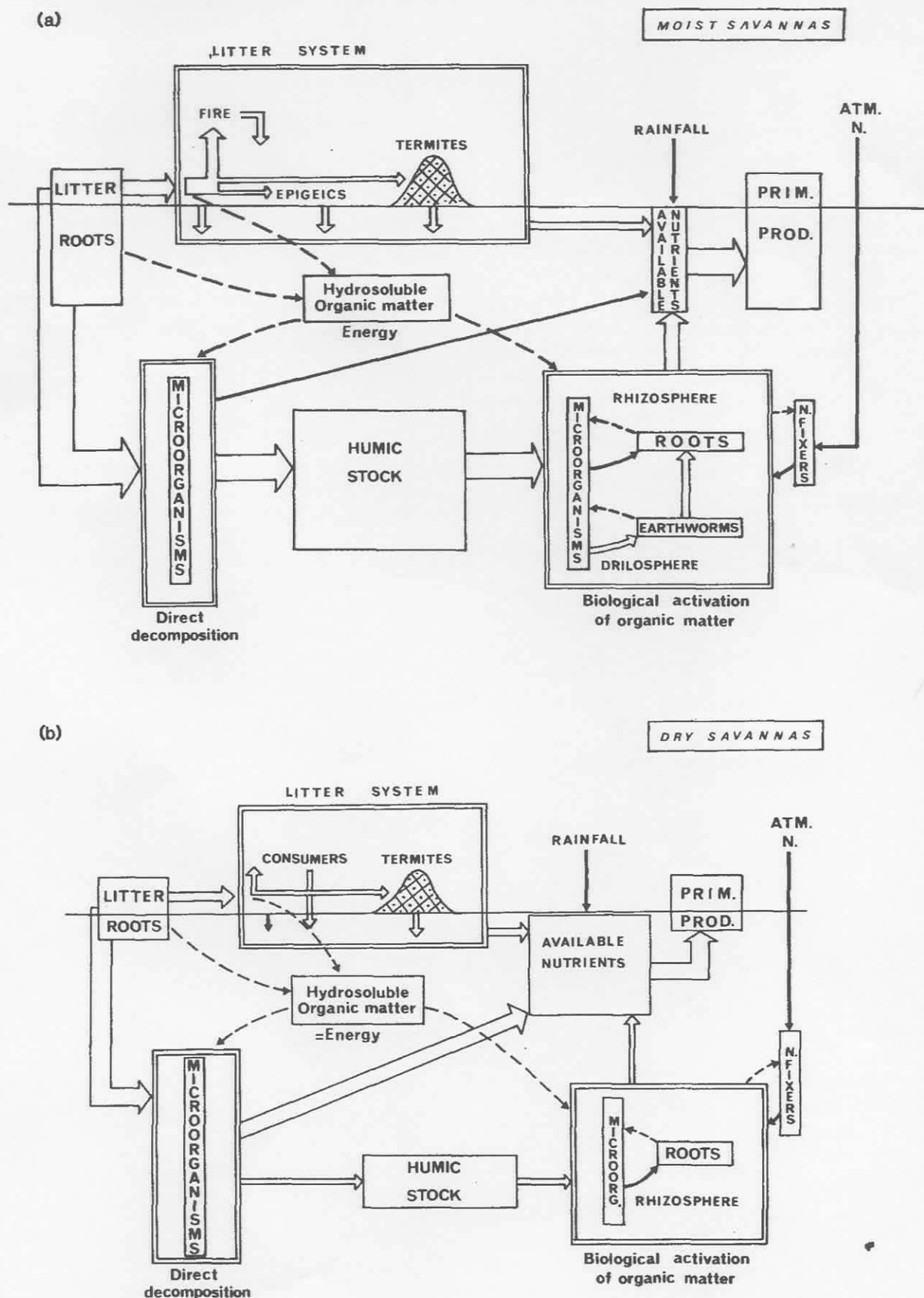


Figure 14. Biological processes involved in nutrient release in (a) moist savannas, (b) dry savannas.

It has been observed that absorbing roots often tend to follow earthworm galleries where microbial activity and mineralization is very active. Activation is thus highly localized in the rhizosphere where nutrients are released at the very contact of the root. Nitrogen fixers are also bound to the rhizosphere, no free azotobacters exist in the soil. Balandreau *et al.* (1976) have shown that ca. $12 \text{ kg ha}^{-1} \text{ yr}^{-1}$ of nitrogen is thus fixed in the rhizosphere of *Loudetia* grasses, which covers almost the half of the nitrogen requirements of the *Loudetia* population ($25 \text{ kg ha}^{-1} \text{ yr}^{-1}$) (Addadie, 1983).

This activation is also regulated throughout the year by the soil water availability and by the chemical status of the soil. As an example, when hydrosoluble organic matter increases in the soil with parallel increase in mineralization, earthworms lower their activity, ingest less soil and the microbial activity in their casts is inhibited. On the contrary, in conditions of low hydrosoluble organic matter and low mineralization, the earthworms ingest greater amounts of soil and microbial activity in their casts increases (Lavelle *et al.*, 1983b).

This biological activation ensures a very strict regulation of the humic stock. The release of nutrients is slow but steady and mostly localized in places where they can be immediately absorbed. This absorption is certainly facilitated by the great development of the root systems. Chapin (1980) has also suggested that, under nutrient stress, roots do not improve their absorbing efficiency but rather tend to enhance their absorbing surfaces. All this can be considered as an adaptation to intense leaching.

It is also clear that soil nutrient availability depends on the nature of the parent material. However, it seems that nutrient release from parent material certainly influences successional processes and the establishment of adapted types of vegetation (and conversely), but once an 'ecosystem' has reached a relatively mature stage, regulation processes within the soil biological system dominate. This is specially true in moist savannas experiencing high leaching. As an example, the older a soil, the more occluded becomes phosphorus (Walker and Syers, 1976) and biological processes only make it available again.

Arid system (Figure 14b)

In arid conditions, litter production often equals root production. As compared to what occurs in moist savannas, the litter system becomes more important. Litter consumption by termites often reaches high values ($> 50\%$) and the rest is directly or indirectly consumed by epigeic animals, including large herbivores. More or less transformed organic matter is thus deposited in the upper horizons of the soil, since the beginning of the rainy season to the core of the dry season onwards.

Cattle and wild mammals are often numerous in arid savannas but do not change the general scheme: they consume green biomass and litter, and most nutrients are released afterwards in their feces which enter the litter system. It is worth noting that termite biomass often averages 10 g m^{-2} (0.1 t ha^{-1} of fresh weight with maximums up to 50 g m^{-2}) (Wood and Sands, 1978); for ungulates, Bourlière (1983b) quotes biomasses varying from 1 to 30 t km^{-2} ($0.01\text{--}0.3 \text{ t ha}^{-1}$) which is very comparable to the figures quoted for termites. Termites are very efficient consumers and producers, they may severely compete with large herbivores (Lepage, 1981).

At the onset of the rainy season, transformed litter, dead roots and dead bodies of micro and macro-organisms are immediately leached. The rather low but pulsed amount of assimilable carbon immediately activates the microflora which produces a relatively high amount of available nutrients. A small fraction of highly condensed humic molecules is added to the low humic stock. It has to be noted that this humic stock is made of more simple complexes than the ones of moist savannas. Its life span is certainly shorter and nutrients fixed in the complexes are more easily released. This low amount of humic stock certainly comes from the low primary production, the immediate mineralization and the lack of soil fauna specialized in humification. The rapid mineralization is needed to cope with the short duration of the growing season and the stock of available nutrients is not leached due to the scarcity of rains.

This adaptation to drought has not induced the same biological regulation system as seen in moist savannas. Soil macrofauna has disappeared and the small rhizosphere system is sufficient to exploit the low humic stock and absorb free nitrogen through nitrogen fixers.

In arid savannas, the high mineral content may be in some cases partly due to the intense evaporation facilitating upwards movements of nutrients from the mother rock. However, the rapid and intense mineralization of the organic matter is favoured by the high temperatures. It has also often been shown that nitrogen mineralization is higher in soils experiencing marked dry periods than in soils more or less constantly humid. Dommergues and Mangenot (1970) had also noted that soil dessication increased the saccharide, hexose and pentose content of the soil. This high mineralization within the whole system is allowed by the absence of leaching and is a clear 'adaptation' to the need that plants have to grow very quickly.

CONCLUSION

It has often been stated that, apart from water status, nutrient availability, particularly nitrogen and phosphorus, was a limiting factor of the fertility of moist or arid savanna soils. In fact, the potential amount of nutrients is not so low but their release is limited by the lack of easily assimilable carbon sources.

In arid savannas, Penning de Vries and Djiteye (1982) concluded that nitrogen was a limiting factor. However, Krul *et al.* (1982) also pointed out that the mineralization of nitrogen by microorganisms implied a large utilization of organic carbon, the resources of which are often weak in these conditions — without speaking of assimilable carbon. In moist savannas, Darici (1978) has shown that bringing small carbon molecules such as gelose activated mineralizing bacteria. These bacteria do not fix the atmospheric nitrogen but decompose the organic matter. Direct inputs of mineral nitrogen do not activate microbial activity and the recycling of organic matter. An inverse effect has even been observed. Kaiser (1983) concluded that the limiting factor in savanna soils is not nitrogen but easily assimilable carbon.

Arid savannas display relatively high amounts of nutrients in the soil. This apparent richness practically corresponds to the major part of available nutrients along the year. The immediate availability of nutrients is allowed by the reduced leaching and enables rapid regrowth of the herbaceous cover. In moist savannas, the measured poorness in nutrients (in fact instantaneous poorness) do not reflect the total flow of nutrients throughout the year. As an adaptation to the intense leaching, nutrients are progressively released all year long as required by plant growth. This release is carried out through a long cycle involving the organic matter stock and through a shorter one directly bound to root decomposition. Both cycles can be compared to the two major 'nutrient strategies' described by Coleman *et al.* (1983); the short and fast cycle reminds the one currently observed in tropical rain forests (Golley, 1983).

One has to be extremely careful when declaring a soil is poor or fertile. A 'fertile' soil could well be very fragile (unprotected stock of nutrients) and a so-called poor soil possess the biological systems enabling an efficient and protected cycling of nutrients able to sustain an high and long lasting production. Fertilization and soil management to increase production should certainly take this point into a great account.

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